PB83-223834

Differential Photosynthetic Inhibition by Ultraviolet Radiation in Species from the Arctic-Alpine Life Zone (Journal Version)

Utah State Univ., Logan

Prepared for

Corvallis Environmental Research Lab., OR

1982

U.S. Department of Commerce
National Technical Information Service
NTIS

TECHNICAL REPORT DATA
(Please read Instructions on the reverse before completir

1. REPORT NO. EPA-600/J-82-337	2.
3. I PB83-223834	
4. TITLE AND SUBTITLE: Differential Photosynthetic Inhibition by Ultraviolet Radiation in Species from the Arctic-Alpine Life Zone (Journal Version)	5. REPORT DATE 1982
	6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S): Martyn M. Caldwell, Ronald Robberecht, Robert S. Nowak, and W.D. Billings	8. PERFORMING ORGANIZATION REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS: Dept. of Range and the Ecology Center, Utah State University, Logan, Utah 84322; Dept. of Botany, Duke University, Durham, North Carolina 27706	10. PROGRAM ELEMENT NO.
	11. CONTRACT/GRANT NO. CR808167
12. SPONSORING AGENCY NAME AND ADDRESS: Environmental Research Laboratory, U.S. Environmental Protection Agency, Corvallis, Oregon 97333	13. TYPE OF REPORT AND PERIOD COVERED extramural
	14. SPONSORING AGENCY CODE EPA/600/02

15. SUPPLEMENTARY NOTES
Robert Worrest, project officer. FTS-420-4578
Published in Arctic and Alpine Research, Vol. 14, No. 3: 195-202, 1982

16. ABSTRACT

Inhibition of photoynthesis and epidermal damage resulting from ultraviolet irradiation were assessed for arctic and alpine plant species. These species were taken from a latitudinal gradient of the arctic-alpine life zone from the Andes to northern Alaska, which spans a steep change in solar UV-B irradiation (280 to 320nm). Ecotypes and species from the Arctic, where solar UV-B flux is very low, were consistently more sensitive to UV radiation than their counterparts from lower latitude alpine regions, where solar UV-B flux is high. Most of the species did not display a change in UV-radiation sensitivity following a 2-wk pretreatment at elevated UV-B irradiance. The difference in photosynthetic inhibition caused by UV irradiation of arctic and alpine ecotypes of Oxyria digyna could not be attributed solely to differences in UV flux penetrating to mesophyll tissues. Further, arctic ecotypes exhibited short-term fluorescence transients indicating damage to the oxidizing side of Photosystem II in the photosynthetic light reaction, whereas there was no indication of this for alpine ecotypes. Thus, there appears to be inherent qualitative and quantitative differences in the UV-radiation sensitivity of photosynthetic systems in arctic and alpine ecotypes.

17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group

REPRODUCED BY
NATIONAL TECHNICAL
INFORMATION SERVICE
U.S. DEPARTMENT OF COMMERCE
SPRINGFIELD, VA. 22161

18. DISTRIBUTION STATEMENT: Release to public	19. SECURITY CLASS *(This Report)* unclassified	21. NO. OF PAGES 9
	20. SECURITY CLASS *(This page)* unclassified	22. PRICE

EPA Form 2220-1 (9-73)

EPA-600/J-82-337
JOURNAL ARTICLE

Arctic and Alpine Research, Vol. 14, No. 3, 1982, pp. 195-202

DIFFERENTIAL PHOTOSYNTHETIC INHIBITION BY ULTRAVIOLET RADIATION IN SPECIES FROM THE ARCTIC-ALPINE LIFE ZONE

MARTYN M. CALDWELL, RONALD ROBBERECHT, AND ROBERT S. NOWAK
Department of Range Science and the Ecology Center, Utah State University Logan, Utah 84322, U.S.A.

W. D. BILLINGS
Department of Botany, Duke University, Durham, North Carolina 27706, U.S.A.

ABSTRACT

Inhibition of photosynthesis and epidermal damage resulting from ultraviolet irradiation were assessed for arctic and alpine plant species. These species were taken from a latitudinal gradient of the arctic-alpine life zone from the Andes to northern Alaska, which spans a steep change in solar UV-B irradiation (280 to 320 nm). Ecotypes and species from the Arctic, where solar UV-B flux is very low, were consistently more sensitive to UV radiation than their counterparts from lower latitude alpine regions, where solar UV-B flux is high. Most of the species did not display a change in UV-radiation sensitivity following a 2-wk pretreatment at elevated UV-B irradiance. The difference in photosynthetic inhibition caused by UV irradiation of arctic and alpine ecotypes of *Oxyria digyna* could not be attributed solely to differences in UV flux penetrating to mesophyll tissues. Further, arctic ecotypes exhibited short-term fluorescence transients indicating damage to the oxidizing side of Photosystem II in the photosynthetic light reaction, whereas there was no indication of this for alpine ecotypes. Thus, there appear to be inherent qualitative and quantitative differences in the UV-radiation sensitivity of photosynthetic systems in arctic and alpine ecotypes.

INTRODUCTION

A steep latitudinal gradient of solar ultraviolet-B radiation exists in the arctic-alpine life zone, even though daily total solar radiation during the growing season is about the same at all points along the gradient (Caldwell et al., 1980). Although the UV-B (280 to 320 nm) radiation reaching the earth's surface comprises less than 0.5% of the total solar energy, it is of potential biological significance for plants because radiation in this waveband can damage nucleic acids and proteins (Caldwell, 1971). Ultraviolet radiation equivalent to that currently received in temperate regions has been demonstrated to depress photosynthetic rates and curtail leaf expansion of some plant species (Bogenrieder and Klein, 1977; Sisson and Caldwell, 1977).

The arctic-alpine life zone extending along the Cordillera from northern Alaska to the high Andes provides a series of ideal sites to observe adaptation to UV-B radiation in plant species of similar growth form and phylogenetic affinity. Solar UV-B radiation increases both with decreasing latitude and with increasing elevation. During the season of maximum solar radiation, the daily biologically effective solar UV-B is seven-fold greater at low-latitude, high-elevation sites than in the Arctic (Caldwell et al., 1980). This gradient is as great as can be expected on the earth's surface.

One indication of plant adaptation to solar UV-B radiation along this gradient is manifested in leaf optical properties. Transmittance of UV-B radiation through the

0004-0851/82/030195-08$01.20
Regents of the University of Colorado

leaf epidermis of species from high-elevation sites in Peru, Venezuela, and Hawaii were reported to be consistently less than 2%, while transmittance was quite variable in species from lower elevation temperate and arctic sites (Robberecht et al., 1980). Epidermal UV-B transmittance of these higher latitude species ranged from less than 2% to as high as 25%. Apparently, the selective pressure for substantial epidermal attenuation of UV-B has not been as great in these higher latitude regions where solar UV-B flux is lower.

Although effective epidermal UV-B attenuation may compensate to some extent for the high solar UV-B irradiance in low-latitude regions, the inherent UV radiation sensitivity of species from different parts of the latitudinal arctic-alpine gradient may also differ. In this study, we investigated depression of photosynthesis by UV-B irradiation in arctic species and closely related species or ecotypes from alpine regions. Acclimation potential to higher UV-B flux was also tested.

METHODS

Populations of several arctic and alpine species were cultivated from seed collected at sites along the latitudinal gradient and the experimental tractability of these was investigated. Subsequent study focused primarily on arctic and alpine ecotypes of *Oxyria digyna*. Species pairs of *Taraxacum* and *Lupinus* from arctic and equatorial alpine sites as well as a few other species from the latitudinal gradient were also utilized. Due to leaf characteristics, not all of these species were suitable for all the measurements or experiments. Nomenclature and areas of seed collection follow. Arctic species collected at various locations on the North Slope of Alaska near sea-level elevation included *Oxyria digyna* (L.) Hill, *Taraxacum lateritium* Dahlstedt, *Lupinus arcticus* S. Wats., *Petasites frigidus* (L.) Franch., and *Cochlearia officinalis* L. spp. *arctica* (Schlecht.) Hult. Alpine populations of *Oxyria digyna* (L.) Hill were collected at various sites in Colorado and California at elevations above 3000 m, *Taraxacum* sect. *Mexicana,* A. J. Richard and *Plantago lanceolata* L. were collected in the Peruvian Andes at 4000 m elevation, *Lupinus meridanus* Moritz came from a site in the Venezuelan Andes at 3000 m elevation, and *Hypochaeris radicata* L. was collected on the island of Maui in Hawaii at 2200 m.

The plants were grown in environmental growth chambers under 6000-W xenon lamps with supplemental UV radiation from fluorescent UV "sunlamps" (Westinghouse FS-40) covered by plastic film filters. Visible irradiance (400 to 700 nm) was approximately 550 μmoles $\cdot$ m^{-2} $\cdot$ s^{-1} during the 14-h photoperiod. With different filters, the UV-B component could be altered to provide different treatments (Figure 1). The lamp system has been previously described (Sisson and Caldwell, 1975).

The spectral composition of the irradiance in the chambers approximated that of the terrestrial solar spectrum. However, a simple comparison of total UV-B flux between the chambers and the natural environment is not warranted because of differences in spectral composition and the pronounced wavelength dependence of biological photoreactions in the UV-B waveband. Therefore, in order to relate UV-B radiation properly in these experimental chambers to conditions in nature, the spectral irradiance in each case was multiplied by a weighting function which describes its potential to effect biological photoreactions. This weighted irradiance, integrated with respect to wavelength, is termed biologically effective UV-B irradiance. It is expressed in units of effective milliwatts per square meter. A generalized plant action spectrum (Caldwell, 1971) was used as a weighting function in these calculations. Ultraviolet spectral irradiance was measured with a modified grating spectroradiometer system (Caldwell et al., 1980). Total photon flux in the visible waveband (400 to 700 nm) was measured with a quantum sensor (LiCor Co.).

Plants were cultured in the low UV-flux chambers under a very low background UV-B irradiance of 7 effective mW $\cdot$ m^{-2} during the entire photoperiod (Figure 1). Even in the Arctic, the vegetation would receive this quantity of UV-B radiation on a daily basis (353 effective J $\cdot$ m^{-2} $\cdot$ d^{-1}) on cloudless days during the growing season. As a high UV-B radiation pretreatment in another chamber, an additional 116.5 effective mW $\cdot$ m^{-2} was given during the middle 6 h of the photoperiod by fluorescent UV lamps filtered with cellulose acetate plastic film (Figure 1). The total daily dose of 2870 effective J $\cdot$ m^{-2} $\cdot$ d^{-1} is close to the maximum total daily UV-B irradiation in high-elevation equatorial environments (Caldwell et al., 1980).

Very high flux irradiation from an unfiltered fluorescent sunlamp was employed in short-term experiments to test plant sensitivity to UV-B radiation. Although this irradiation is substantially greater than that received in low-latitude, high-elevation environments and includes a small amount of radiation below 290 nm, it does provide a short-term irradiation test to assay photosynthetic and epidermal damage with high experimental repeatability. These sensitivity tests were conducted on fully expanded leaves of established plants, while the remainder of the plant was shielded from UV irradiation. Sensitivity assays for photosynthetic inhibition and epidermal damage were conducted on plants taken directly from the low UV-B flux environmental chamber and in some experiments also on plants which had received a 2-wk pretreatment period in the high UV-B flux chamber.

Photosynthesis and transpiration of individual leaves were simultaneously measured in a plant gas exchange system before and after a 15-h, very high UV-flux irradiation. In this gas exchange system, CO_2 and water vapor

concentrations were measured by infrared gas analysis (Beckman Instruments, Inc.) and capacitance humidity sensors (Vaisala Co.), respectively. Flow rates were determined with a pneumotachometer (Hans Rudolph Co.) and a pressure transducer (Validyne Co.). A small leaf cuvette, patterned after that of Patterson et al. (1977), was enclosed in a larger cuvette with a Peltier heat exchanger (Siemens Co.). Intercellular CO_2 concentrations were calculated and the ambient CO_2 concentrations around the leaf adjusted to maintain a constant intercellular CO_2 concentration for all photosynthetic assays (Caldwell et al., 1977). All photosynthetic measurements were conducted at a leaf temperature of 20° (±1°) and a photon flux density of 1100 μmole · m^{-2} · s^{-1} (400 to 700 nm) which was sufficient to provide for light saturation of photosynthesis in all of these plants.

The high flux irradiation system used for inflicting photosynthetic depression was used to determine the

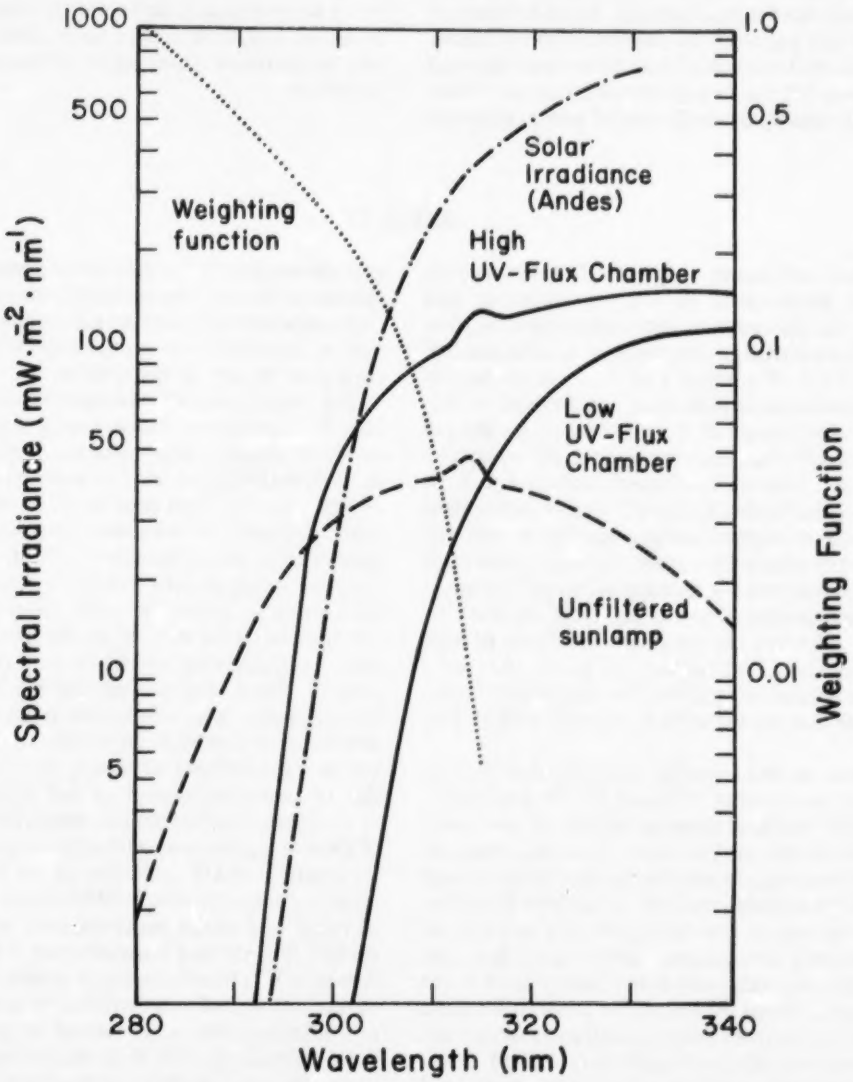

FIGURE 1. Ultraviolet spectral irradiance reaching the plants in the low UV-flux environmental growth chamber, in the middle 6 h of the photoperiod in the high UV-flux chamber, and under the unfiltered fluorescent sunlamp for short-term inactivating irradiation. Noontime solar spectral irradiance at the season of maximum solar altitude at 3560 m elevation in Venezuela (from Caldwell et al., 1980) and the generalized plant weighting function are also shown.

threshold UV-B dose required for minimal perceptible epidermal damage. A template system was employed with small test strips on the leaf surface exposed to a range of irradiation exposure times. The damage was assessed microscopically as glazing or slight bronze coloration of the epidermal surface 24 h after the exposure period.

The epidermal UV transmittance of leaves was determined on freshly removed epidermal tissue segments using an integrating sphere/spectroradiometer system (Robberecht and Caldwell, 1978). Intact fresh epidermal tissue of sufficient size for analysis (3 mm in diameter) could be removed from only a few of the test species. Both arctic and alpine ecotypes of *Oxyria digyna* were particularly tractable for this analysis. As an estimate of the capacity of leaf pigments to absorb UV-B radiation, methanol-water-HCl extracts of leaf tissues were assayed for absorbance at 305 nm in a spectrophotometer. These pigments were primarily of the flavonoid group, although a few other compounds that absorb UV-B were included in this extract (Caldwell, 1968; Wellmann, pers. comm., 1981). Measurements of epidermal UV transmittance and pigment absorbance were made on fresh, turgid leaves that were not exposed to inactivating UV radiation.

Fluorescence transients (Kautsky effect) of intact leaves were used to indicate if that component of the photosynthetic light reaction known as Photosystem II was affected by UV irradiation. Fluorescence transients of arctic and alpine ecotypes of *Oxyria digyna* were measured with a fluorometer probe and oscillograph (Brancker Research, Ltd. and Varian Co., respectively) following the pattern described by Schreiber et al. (1975). Fluorescence was induced in dark-adapted leaves with continuous radiation at 670 nm from a photodiode and fluorescence was measured at wavelengths longer than the induction radiation.

RESULTS

Photosynthetic inhibition by UV irradiation was consistently more pronounced in arctic populations and species of *Oxyria, Taraxacum,* and *Lupinus* than in their counterparts from alpine environments at middle and low latitudes ($p<0.05$). A summary of two sets of experiments on photosynthetic inhibition is presented in Figure 2. The first set involved the use of plants cultured only in the low UV-flux chamber before the sensitivity assay. The second was designed to determine if a 2-wk pretreatment period under a high UV-B flux (equivalent to that received in high-elevation, equatorial regions) would reduce the sensitivity. Only *Plantago lanceolata* exhibited less photosynthetic damage in this pretreatment experiment when compared to controls from the low UV-flux chamber. All other species (from either low or high UV-flux pretreatment regimens) exhibited the same photosynthetic inhibition as in the first experiment. Thus, the data of the two experiments were combined in Figure 2.

The sensitivity of these species for epidermal damage is indicated as the number of hours of UV irradiation required to elicit minimal damage in 50% of the leaves of each species (Table 1). This level of damage was calculated from linear regressions for the leaf series in each experiment. (The average coefficient of determination, r^2, for these regressions was 0.95.) For the ecotypes of *Oxyria digyna* and the *Lupinus* species pair, leaf epidermal damage was exhibited significantly sooner for leaves of the arctic plants than of plants from alpine areas when the 50% levels from these experiments were compared in a one-way analysis of variance ($p<0.05$). However, when comparing the entire group of arctic and alpine species tested, there was no statistically significant difference. As with photosynthetic inhibition, a second experimental series was conducted to determine if pretreatment at a high UV-B irradiation for 2 wk would mitigate the sensitivity for epidermal damage. The results of this second series were essentially identical to those of the first series and indicated no statistically significant reduction of sensitivity due to the high UV-B radiation pretreatment in any of the species.

The mean spectral UV transmittance of epidermal tissues from arctic and alpine ecotypes of *Oxyria digyna* is shown in Figure 3 along with the average whole-leaf pigment (flavonoid) content expressed as extract absorbance at 305 nm. The difference in UV-B epidermal transmittance between the two ecotypes was proportionately greater than the difference in UV-B-absorbing pigment concentrations of entire leaves. In addition to flavonoid absorption in epidermal cells, differences in epidermal UV transmittance may be attributed to epidermal thickness, cuticular characteristics, and other cellular compounds. Thus, a direct correlation between epidermal transmittance and whole-leaf pigment concentrations would not be expected. Nevertheless, the lower epidermal UV-B transmittance of alpine ecotypes may be in part due to greater quantities of leaf flavonoids.

To determine if the greater sensitivity of arctic ecotypes of *Oxyria digyna* is attributable simply to differences in attenuation of UV radiation in the leaf epidermis, the relative photosynthetic inhibition and epidermal damage of arctic and alpine ecotypes were adjusted to account for UV-B epidermal transmittance in Figure 3. Since epidermal UV-B transmittance is a measure of the attenuation of UV-B radiation within the epidermis, the degree of epidermal damage is related to epidermal transmittance. Similarly, UV-B radiation-induced damage to photosynthesis would be related to the amount of UV-B radiation which penetrates through the epidermis. (Epidermal damage was calculated as the reciprocal of threshold time for minimal damage. Both epidermal damage and photosynthetic inhibition were divided by the

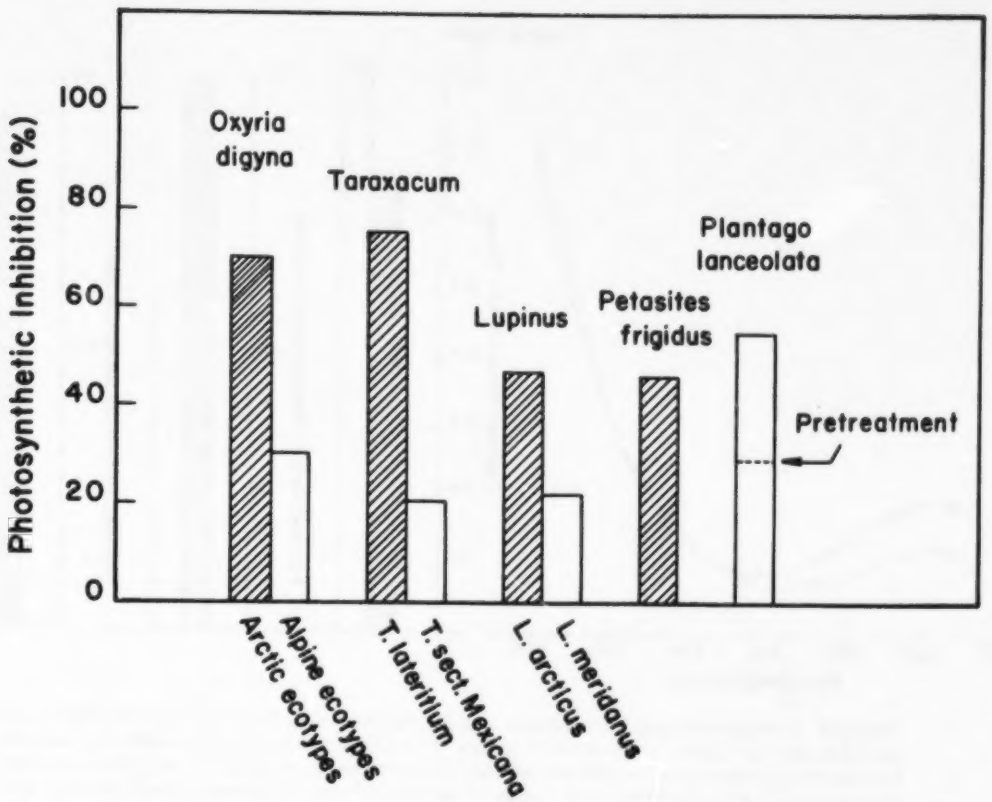

FIGURE 2. Relative inhibition of net photosynthesis following a 15-h irradiation under unfiltered sunlamps for arctic (hatched bars) and alpine (open bars) ecotypes and species from the latitudinal gradient based on preirradiation photosynthetic rates. Photosynthetic inhibition was significantly greater in arctic plants of *Oxyria*, *Taraxacum*, and *Lupinus* compared to their alpine counterparts in a two-tailed *t* test ($p<0.05$). This figure summarizes results of two experiments. In the first experiment, all plants were cultured in the low UV-flux chamber before the short-term inactivating irradiation. In the second experiment, half of the plants were cultured in the low-flux chamber and the other half exposed to a 2-wk pretreatment period in the high UV-flux chamber before the short-term inactivating irradiation. The results of both experiments yielded identical results except for *Plantago lanceolata* which exhibited less inhibition following the high-UV irradiation pretreatment as indicated by the dashed line. A minimum of 15 plants was tested for each species and ecotype.

TABLE 1

Ultraviolet radiation exposure required to elicit minimal perceptible epidermal damage in 50% of the leaves of each species[a]

Arctic species	Exposure (h)	(*n*)	Alpine species	Exposure (h)	(*n*)
Oxyria digyna	10.6	27	*Oxyria digyna*	15.3	27
Taraxacum lateritium	9.2	16	*Taraxacum* sect. *Mexicana*	8.4	16
Lupinus arcticus	2.6	16	*Lupinus meridanus*	7.9	16
Petasites frigidus	3.1	18	*Hypochaeris radicata*	5.3	9
Cochlearia officinalis	7.0	9	*Plantago lanceolata*	4.1	16

[a]The total number of plants tested for each species is also indicated (*n*). Ecotypes of *Oxyria digyna* and the species of *Lupinus* differed significantly ($p<0.05$).

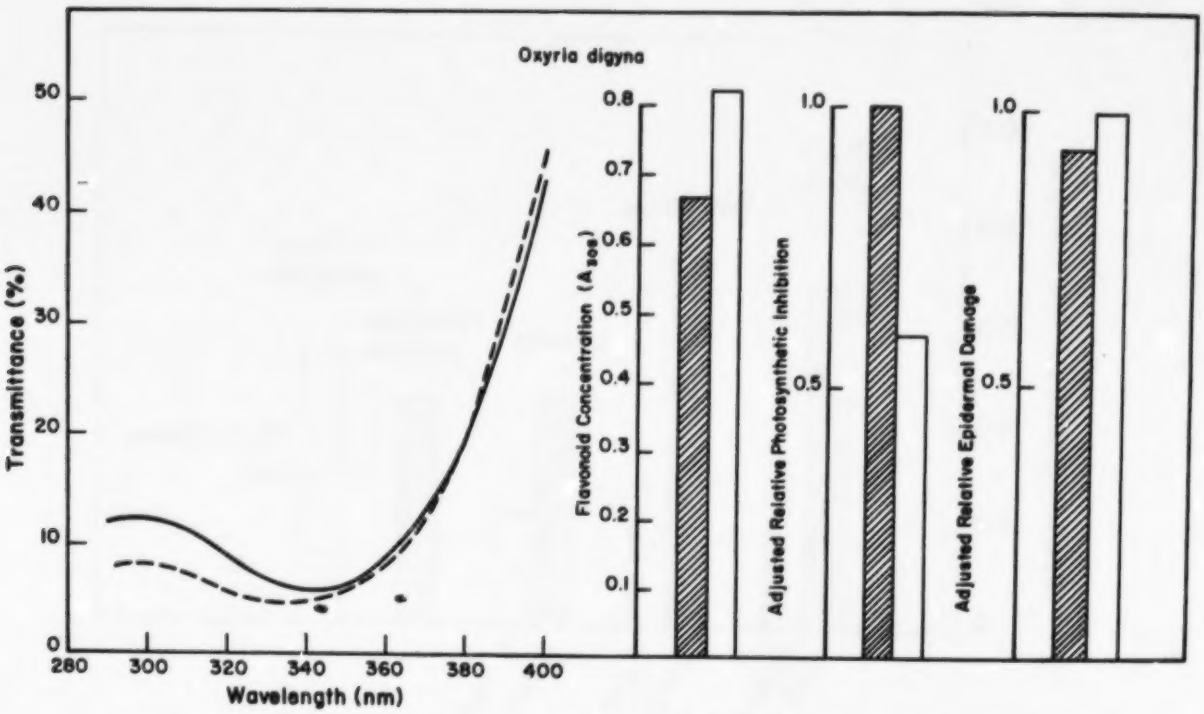

FIGURE 3. Average epidermal transmittance of arctic (solid lines) and alpine (intermittent line) ecotypes of *Oxyria digyna*. Pigment concentrations (primarily flavonoids) of whole-leaf extracts of arctic (hatched bar) and alpine (open bar) ecotypes are indicated as extract absorbance at 305 nm. Differences between ecotypes in UV-B transmittance and flavonoid pigment concentrations were significant at $p<0.05$ in a two-tailed t test. Also shown are the relative photosynthetic inhibition (from Figure 2) and epidermal damage (reciprocal of threshold irradiation time from Table 1) adjusted for equivalent UV flux reaching the mesophyll tissues by taking UV-B epidermal transmittance into account. Adjusted photosynthetic damage is significantly different between the ecotypes at $p<0.05$ whereas adjusted epidermal damage is not.

epidermal UV-B transmittance of the respective ecotype and then normalized.) Following adjustment for epidermal UV-B transmittance, epidermal damage of the two ecotypes was not significantly different. However, for photosynthetic inhibition, the arctic ecotypes still exhibited significantly greater sensitivity even after accounting for differences in penetration of UV-B radiation to mesophyll tissues (analysis of variance of ratios, $p<0.05$).

The qualitative nature of damage to the photosynthetic light reaction is indicated by specific fluorescence transients for arctic and alpine ecotypes of *Oxyria digyna* in Table 2. The changes in transient intervals are summarized for leaves tested before and after UV irradiation. The transients I and P refer to different stages of the characteristic time course of fluorescence from a leaf. When a leaf previously held in darkness is exposed to strong continuous illumination, fluorescence increases from an initial level to an intermediate level (I) within milliseconds, and then somewhat more slowly to a peak (P) at approximately 1 s after initiation of illumination. Fluorescence then decays to subsequent transient stages (Papageorgiou, 1975). It is the average interval between I and P, expressed in arbitrary units, that is presented

TABLE 2
Magnitude of interval between intermediate and peak (I-P) fluorescence transients for ecotypes of Oxyria digyna *(relative units) before and after UV irradiation*

	I-P	*n*
Arctic ecotypes		
Pre-irradiation	43.9 *	40
Post-irradiation	31.5	
Alpine ecotypes		
Pre-irradiation	34.8	40
Post-irradiation	38.8	

*Significant difference between pre- and postirradiation at $p<0.01$, two-tailed t test.

in Table 2. A reduction of the interval between I and P would indicate damage on the oxidizing side of Photosystem II, such as reduced water-splitting activity. On the other hand, an increase in the interval between I and P would indicate a greater pool of reduced plastoquinone, which may be linked to phenomena such as inhibited electron transport capacity between the photosystems (Schreiber et al., 1978). Arctic ecotypes of *Oxyria digyna*, in which net photosynthesis had been significantly depressed by UV irradiation (Figure 2), exhibited a significant decrease in the I-P transient interval following the UV irradiation (Table 2). In contrast, a significant UV-induced photosynthetic depression in alpine ecotypes of *Oxyria* was not accompanied by a decrease of the I-P interval. Thus, the nature of damage to the photosynthetic system of arctic and alpine ecotypes appeared to differ qualitatively as well as quantitatively.

DISCUSSION

As might be anticipated from the steep latitudinal gradient of biologically effective solar UV-B radiation in the arctic-alpine life zone, arctic species appear to be inherently more sensitive to UV radiation than alpine species from lower latitudes. Furthermore, based on the comparison of arctic and alpine ecotypes of *Oxyria digyna*, the inherent difference in sensitivity appeared not to be simply a matter of a difference in UV-shielding of the mesophyll tissues by the epidermis (Figure 3). These results differ from the studies of Van et al. (1977) who reported that the UV-B inhibition of several component photosynthetic reactions of isolated chloroplasts was the same for three species which varied considerably in UV-B inhibition of net photosynthesis for intact leaves. They concluded that ultraviolet screening by outer plant tissue layers was apparently the sole determinant of differences in UV sensitivity of these species. Some of the difference in sensitivity of the ecotypes of *Oxyria* may be due to arrangement of chloroplasts and UV absorbing compounds within the mesophyll. Yet, the large difference in photosynthetic inhibition which was still apparent after adjustment for UV-B radiation reaching the mesophyll tissues (Figure 3) and the qualitative differences in photosynthetic damage indicated by fluorescence transients (Table 2), suggest that the difference in radiation sensitivity between arctic and alpine ecotypes of this species involves more than simply unequal radiant flux reaching physiological targets in the chloroplasts. The photosynthetic UV-radiation sensitivity of the leaf mesophyll appears to be inherently different in arctic and alpine ecotypes of *Oxyria*.

In contrast, for epidermal damage, an adjustment for UV epidermal transmittance indicated similar damage thresholds for arctic and alpine populations (Figure 3). Epidermal tissue damage has been shown to be photoreactivable, i.e., the lesions are greatly lessened if the leaf is exposed to visible radiation concomitant with or immediately following the UV-B irradiation (Caldwell, 1968; Cline et al., 1969). Since photoreactivation is specific to the repair of nucleic acid damage (Setlow, 1966), the responsible chromophores for epidermal damage are nucleic acids within the epidermal cells. Apparently the nucleic acids of epidermal cells of arctic and alpine ecotypes of *Oxyria* are equally susceptible to UV-B irradiation if an allowance for epidermal UV transmittance is made. The chromophores for photosynthetic damage are not known explicitly. Several possible targets have been suggested such as plastoquinone (Mantai and Bishop, 1967), Photosystem II reaction centers (Yamashita and Butler, 1968), and thylakoid membranes (Mantai et al., 1970), but available evidence suggests that nucleic acids are not involved as primary chromophores (Caldwell, 1981). Thus, epidermal damage and photosynthetic damage are fundamentally different photobiological reactions.

The higher dose rates and the somewhat different wavelength composition of the irradiation used in these experiments (Figure 1) likely caused greater photosynthetic depression in these experiments than would be anticipated in the field even in low-latitude, high-elevation regions. The short-term high flux UV irradiation in these experiments was employed to effect large depressions in photosynthesis in order to elicit clear differences in sensitivity among ecotypes and species. Thus, the complicating factors affecting photosynthesis such as leaf aging that would occur if the same UV dose was administered over a longer period of time were avoided. (If the same biologically effective dose was provided at rates to be expected in low-latitude, high-elevation environments, it would take nearly 3 d to deliver the dose used in the photosynthesis depression experiments—7965 effective $J \cdot m^{-2}$.) Another reason why plants in the field may be less affected by solar UV irradiation than in these experiments is that epidermal transmittance of species examined in the field has been shown to be lower than when the same species are grown under artificial conditions (Robberecht and Caldwell, 1978; Robberecht et al., 1980). Although solar UV-B radiation is likely not a major constraint on primary productivity in alpine areas at present, the consistently large difference in photosynthetic damage between ecotypes or species pairs at different locations on the latitudinal gradient of the arctic-alpine life zone (Figure 2) and the consistently low UV epidermal transmittance at low latitudes (Robberecht et al., 1980) suggest solar UV-B irradiation has been an evolutionary selective force in at least a portion of this life zone.

Atmospheric ozone depletion would lead to enhanced solar UV-B radiation flux at all locations on the latitudinal gradient. Whether plant species can adapt to yet higher UV-B flux in the time frame of a few decades over

which much of the ozone depletion is predicted to occur (National Academy of Sciences, 1979) is an open question. Short-term UV radiation pretreatments as employed in these experiments yielded no apparent acclimatization for most species. Nevertheless, prolonged pretreatment regimes might elicit an adaptive response. The apparent genetically based components of UV radiation sensitivity in the photosynthetic systems of arctic and alpine ecotypes would likely be much slower to respond to the process of natural selection.

ACKNOWLEDGMENTS

This research was supported by grants from the National Science Foundation (DEB 76-22381), the Environmental Protection Agency, and the National Aeronautics and Space Administration. The technical and research assistance of L. B. Camp and S. D. Flint of Utah State University was instrumental in this research. We are also grateful to Shirley Billings for seed collection and organization.

REFERENCES CITED

Bogenrieder, A. and Klein, R., 1977: Die Rolle des UV-Lichtes beim sog. Auspflanzungsschock von Gewachshaussetzlingen. *Angewandte Botanik,* 51: 99-107.

Caldwell, M. M., 1968: Solar ultraviolet radiation as an ecological factor for alpine plants. *Ecological Monographs,* 38: 243-268.

———, 1971: Solar UV irradiation and the growth and development of higher plants. *In* Giese, A. C. (ed.), *Photophysiology.* Vol. 6. New York: Academic Press, 131-177.

———, 1981: Plant response to ultraviolet radiation. *In* Lange, O. L., Nobel, P. S., Osmond, C. B., and Ziegler, H. (eds.), *Encyclopedia of Plant Physiology.* Vol. 12A. *Physiological Plant Ecology I. Responses to the Physical Environment.* Berlin: Springer-Verlag, 169-198.

Caldwell, M. M., Osmond, C. B., and Nott, D. L., 1977: C_4 pathway of photosynthesis at low temperature in cold-tolerant *Atriplex* species. *Plant Physiology,* 60: 157-164.

Caldwell, M. M., Robberecht, R., and Billings, W. D., 1980: A steep latitudinal gradient of solar ultraviolet-B radiation in the arctic-alpine life zone. *Ecology,* 61: 600-611.

Cline, M. G., Conner, G. I., and Salisbury, F. B., 1969: Simultaneous reactivation of ultraviolet damage in *Xanthium* leaves. *Plant Physiology,* 44: 1674-1678.

Mantai, K. E. and Bishop, N. I., 1967: Studies on the effects of ultraviolet irradiation on photosynthesis and on the 520-nm light-dark difference spectra in green algae and isolated chloroplasts. *Biochimica et Biophysica Acta,* 131: 350-356.

Mantai, K. E., Wong, J., and Bishop, N. I., 1970: Comparison studies on the effects of ultraviolet irradiation on photosynthesis. *Biochimica et Biophysica Acta,* 197: 257-266.

National Academy of Sciences, 1979: *Protection against Depletion of Stratospheric Ozone by Chlorofluorocarbons.* Washington, D.C. 392 pp.

Papageorgiou, G., 1975: Chlorophyll fluorescence: An intrinsic probe of photosynthesis. *In* Govindjee (ed.), *Bioenergetics of Photosynthesis.* New York: Academic Press, 319-371.

Patterson, D. T., Bunce, J. A., Alberte, R. S., and Van Volkenburgh, E., 1977: Photosynthesis in relation to leaf characteristics of cotton from controlled and field environments. *Plant Physiology,* 59: 384-387.

Robberecht, R. and Caldwell, M. M., 1978: Leaf epidermal transmittance of ultraviolet radiation and its implications for plant sensitivity to ultraviolet-radiation induced injury. *Oecologia,* 32: 277-287.

Robberecht, R., Caldwell, M. M., and Billings, W. D., 1980: Leaf ultraviolet optical properties along a latitudinal gradient in the arctic-alpine life zone. *Ecology,* 61: 612-619.

Schreiber, U., Groberman, L., and Vidaver, W., 1975: Portable, solid-state fluorometer for the measurement of chlorophyll fluorescence induction in plants. *Review of Scientific Instruments,* 46: 538-542.

Schreiber, U., Vidaver, W., Runeckles, V. C., and Rosen, P., 1978: Chlorophyll fluorescence assay for ozone injury in intact plants. *Plant Physiology,* 61: 80-84.

Setlow, R. B., 1966: Cyclobutane-type pyrimidine dimers in polynucleotides. *Science,* 153: 379-386.

Sisson, W. B. and Caldwell, M. M., 1975: Lamp/filter systems for simulation of solar UV irradiance under reduced atmospheric ozone. *Photochemistry and Photobiology,* 21: 453-456.

———, 1977: Atmospheric ozone depletion: Reduction of photosynthesis and growth of a sensitive higher plant exposed to enhanced UV-B radiation. *Journal of Experimental Botany,* 28: 691-705.

Van, T. K., Garrard, L. A., and West, S. H., 1977: Effects of 298-nm radiation on photosynthetic reactions of leaf discs and chloroplast preparations of some crop species. *Environmental and Experimental Botany,* 17: 107-112.

Wellmann, E., 1981: Personal communication. Biological Institute 11, University of Freiburg, Schanzlestrasse 9-11, 7800 Freiburg, Federal Republic of Germany.

Yamashita, T. and Butler, W. L., 1968: Inhibition of chloroplasts by UV-irradiation and heat-treatment. *Plant Physiology,* 43: 2037-2040.

Ms submitted September 1981